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Ecogeographic patterns in a mainland-island system in Northern Europe as inferred from the rove beetles (Coleoptera: Staphylinidae) on Læsø island

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Abstract. Rove beetles (Staphylinidae) are used to explore the forces that shaped the terrestrial fauna on Læsø, a young ca. 3000 year old Danish oceanic island located in the Kattegat strait between mainland Denmark and Sweden. We compile a detailed list of species of rove beetles for Læsø (328 species) and the surrounding Danish and Swedish regions (altogether 1075 species), which includes a standardized inventory of their body sizes, and the habitat and microhabitat preference of each species. The composition of the fauna on Læsø and adjacent mainland regions points to North-Eastern Jutland as the main source of the rove beetles on Læsø. Although large beetles are more active and likely to disperse than small beetles, there is no bias towards large species on the island indicating that the sea separating Læsø from the mainland has not been a barrier for rove beetle dispersal. The statistical analysis of the habitat and microhabitat preferences of the species of the entire system studied has shown that Læsø, compared to the mainland areas, is distinctly more dominated by ecological generalists, especially by species adapted to ephemeral, temporary humid microhabitats. Presumably, the mosaic of mostly dry open habitats available on Læsø filters for species, that are able to populate these suboptimal habitats via patches of humid but ephemeral microhabitats. A comprehensive eco-faunistic dataset for the Staphylinidae compiled for this study is the first modern account of the rove beetle fauna on the Danish island of Læsø.

INTRODUCTION

In this paper we aim to capture and measure patterns that give insights into the forces determining insect faunas and communities in a given area or a habitat. Understanding these driving forces, which include the capacity of insect species to disperse and establish in new geographic areas and habitats, are basic for studies on ecology, evolutionary biology or biogeography, because insects are a mega-diverse group and dominate modern biotas in terms of the number of species, abundance and their ecological effect. This makes it difficult to unravel the interplay between morphological, physiological and behavioral traits of an insect species and its biotic and abiotic environments (e.g., Lester et al., 2007; Clobert et al., 2012; Slatyer et al., 2013). Well-known local insect faunas with fine presence/absence data and an abundance of bionomic records for a large number of species occurring in a limited area provide simple models for studying ecogeographic patterns that help understand these relationships. This is especially true

for regions that include both large areas of mainland and islands, i.e. where inhospitable sea barriers clearly partition a study area into a number of units. The North European beetle (Coleoptera) fauna is highly suitable for such studies. It is rich in species and regarded as one of the best known in the world. It provides ecological information on thousands of species distributed across diverse landscapes on the mainland and many islands.

Here we focus on a subset of this fauna delimited by the family of rove beetles (Staphylinidae) (Fig. 1) inhabiting the Danish island Læsø and the surrounding mainland areas of Denmark and southern Sweden (Fig. 2). Rove beetles are a good model group for exploring interactions between species and their environment, because they occur in just about every terrestrial habitat, populate diverse microhabitats and display a wide range of morphological and biological adaptations (Thayer, 2016). Læsø was chosen because it is a young oceanic island with a mosaic of different habitats and microhabitats. This island has never had

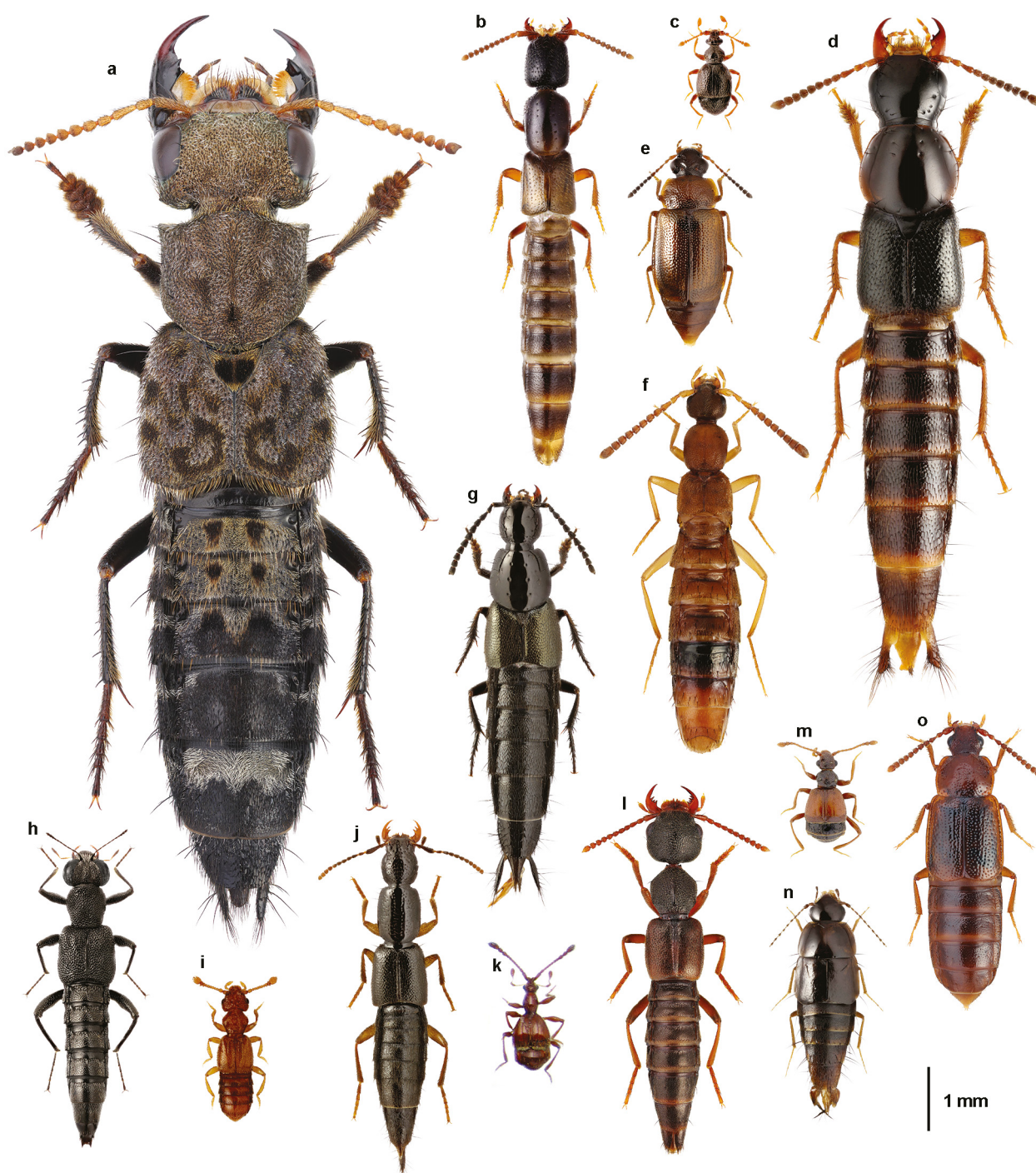


Fig. 1. Exemplar species of rove beetles (Staphylinidae) recorded on Læsø Island. a – *Ontholestes murinus*, b – *Gyrophypnus angustatus*, c – *Bryaxis bulbifer*, d – *Quedius xanthopus*, e – *Anthobium atrocaphalus*, f – *Drusilla canaliculata*, g – *Philonthus carbonarius*, h – *Stenus juno*, i – *Euplectus karstenii*, j – *Octhephilum fracticornis*, k – *Pselaphus heisei*, l – *Rugilus rufipes*, m – *Rybaxis longicornis*, n – *Habrocerus capillaricornis*, o – *Acidota cruentata*. Photographs from www.zin.ru/Animalia/Coleoptera by K.V. Makarov.

any land connections with its surrounding mainland areas, but has a rich insect (and rove beetle) fauna despite the presence of a significant water barrier separating it from those areas. Together with the surrounding mainland, Læsø is an ideal area for studying ecological filtering associated with the colonization of the island by insects with certain traits. We first aim to investigate (1) whether the rove beetle fauna on Læsø is a random accumulation of species or if it is more similar to a certain mainland area(s).

To find out which traits facilitated the rove beetle species dispersal and colonization of Læsø, we (2) determine if there is any filtering of the fauna of Læsø favouring large or small species compared to the surrounding mainland. Jenkins et al. (2007) found a difference in body size between active and passive fliers in many insect taxa, with small species dispersing over shorter distances and more passively, while large species disperse actively and further. Evidence from capture-recapture experiments at the

landscape scale also show that large species of dung beetles disperse between habitat patches more frequently than small species (Roslin, 2000). Indeed, measuring the flight ability is an ideal proxy for inferring the dispersal capacity of the rove beetles that have colonized Læsø. However, this was not possible in this study as all rove beetle species inhabiting Læsø have wings and a thorough population level study of the wing polymorphism within the entire study area would be required. Due to these practical limitations, at this stage we used body size.

Finally, we want to establish if there has been any filtering of the rove beetle fauna on Læsø that has favoured particular ecological group(s) of species with respect to their (3) habitat and (4) microhabitat preferences. Species living in homogeneous environments, such as mesophilous insects living in permanently moist layers of forest leaf litter in mature forests, are commonly believed to be poor dispersers. For example, flight has been proven unnecessary and therefore costly in these continuously stable environments (Roff, 1990; Wagner & Liebherr, 1992). On the contrary, insects living in ephemeral microhabitats scattered throughout the landscape, such as dung, carrion, or compost are often good flyers as they constantly move between patches of substrate with available shelter and food sources (Skidmore, 1991). By focusing on the habitat and microhabitat requirements of rove beetles we use them as a proxy for understanding species ability to disperse and colonize new areas. This approach has been used in various studies on diverse insect groups (Soininen et al., 2007; Qian, 2009; Jiménez-Valverde et al., 2010; Gómez-Rodríguez et al., 2015). The concepts of habitat and microhabitat are complex and somewhat overlapping, especially when considering rove beetles for which the bionomics are described only verbally with more or less detail. In spite of the all these limitations we hope that the ecogeographic patterns of the rove beetle colonization of Læsø explored using the listed four research goals will contribute to a better understanding of the North European beetle fauna, as well as insect faunas and ecological communities in general.

METHODS

Study area

The study area (Fig. 2) consists of the oceanic island Læsø and adjacent mainland regions in Denmark (NE Jutland, E Jutland, Funen, NW Zealand, and NE Zealand) and Sweden (Skåne, Halland, Bohuslän, and Vestra Gotland) on which the composition of habitats varies due to difference in geology, climate and effects of the Quaternary glaciation (de Brogniez et al., 2015). These regions are used as districts in coding species distributions in the beetle catalogues mentioned below, and in our analyses. We can roughly unite them based on soil properties (Olsson, 1999; Petersen, 2010) into three groups supporting different types of habitats. (1) The Southwestern part (E Jutland, Funen, NW Zealand, NE Zealand and Skåne) is dominated by deciduous forest, grassland and agricultural land characteristic of humus rich soils. (2) The Northeastern part (Halland, Bohuslän and Vestra Gotland) has poorer soils and therefore supports coniferous forests, meadows and grassland. And finally, (3) the Northwestern part (NE Jutland and Læsø) is largely formed by a recent rising of the sea

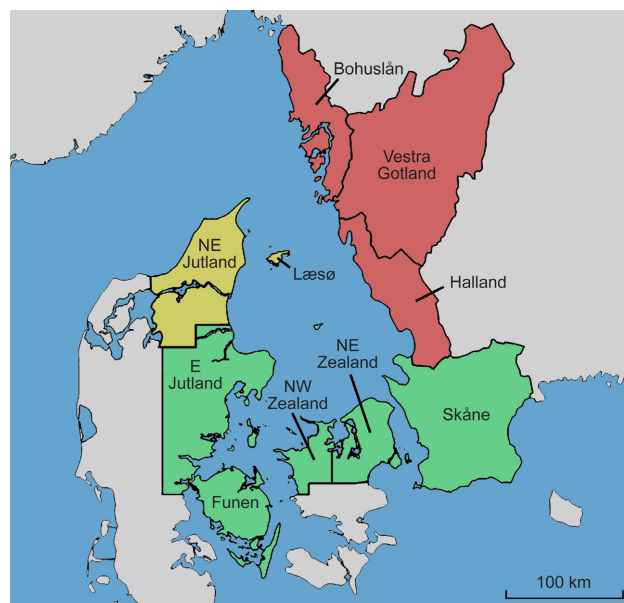


Fig. 2. Map of the study area showing Læsø island and surrounding mainland regions. Different colours indicate different soil properties (Olsson, 1999; Petersen, 2010) supporting different habitats: Southwestern part, green (E Jutland, Funen, NW Zealand, NE Zealand, and Skåne) dominated by deciduous forest, grassland and agricultural land characteristic of humus rich soils; Northeastern part, red (Halland, Bohuslän, and Vestra Gotland) has poorer soils and therefore supports coniferous forests, meadows and grassland; Northwestern part, yellow (NE Jutland and Læsø) largely formed by recent rising of the sea floor and has the poorest soils and habitats such as heathland and coniferous plantations.

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Læsø is an island of 118 km², situated 20 km off the Eastern coast of Jutland, 40 km West of the Southwestern coast of Sweden and 140 km from the North of Zealand. Due to tectonic movements the island arose from the sea no more than 3000 years ago (Hansen 1994, 1995). The island is gradually growing as the sea floor continues to rise and sand is naturally being deposited around the perimeter of the island. This has caused a natural succession promoting salt marshes and heathland in newly raised areas, which are gradually being replaced by scrub and forest on the older parts of the island. Noteworthy is that during the 18th century all the forest on Læsø was cleared to make fire wood for the salt production on the island. This meant that for more than 200 years Læsø consisted of a somewhat harsh aeolian landscape exposed to drifting sand (Hansen, 1994). In 1940 a government-supported reforestation of the island was initiated to stop sand drifting. Initially it was mostly pine trees (*Pinus mugo* and *Pinus sylvestris*) that were planted, but later many spruce and fir trees were also introduced (Johannsen et al., 2013). Currently the island consists of a mixture of pine plantations, heathland, salt marshes, small areas of swamp and oligotrophic lakes, as well as large areas of arable land and pastures grazed by livestock. Ships and ferries routinely visit the island, mainly from the Danish side, facilitating human-introductions of insects. Currently a ferry to Vesterø Havn on Læsø is running three times daily from Frederikshavn (NE Jutland, Denmark).

Data on the species

The list of species and their attributes used in this study was assembled from published checklists of Coleoptera for Denmark (Hansen, 1996) and Sweden (Lundberg, 2006), including recent

additions, with the most up-to-date list of species of rove beetles on Læsø presented here. The Danish and Swedish species lists present records for each species for several faunistic districts, thus providing an accurate approximation of the actual distribution of each species in the area. The checklist of Danish beetles was initiated by Victor Hansen (Hansen, 1964) and published as a succinct catalogue by Michael Hansen (Hansen, 1996). It has been updated periodically ever since (latest update, Hansen & Jørum, 2014). Hansen (1996) subdivided the Danish beetle fauna into 11 faunistic districts based on Enghoff & Nielsen (1977). The checklist of Swedish beetles was originally published by Lundberg & Gustafsson (1995) and revised by Lundberg (2006) to include all species of beetle recorded in Sweden. In these catalogues, the Swedish beetle fauna is also recorded for 25 historical provinces (“*landskap*” in Swedish).

Since Hansen (1996) generalized species distributions in terms of a list of faunistic districts a given species occurred in, and since Læsø is part of the NE Jutland faunistic district, its beetle fauna cannot be obtained from that catalogue. For the same reasons this catalogue does not provide information on species that occur only in the mainland area of the NE Jutland faunistic district. However, two separate lists of species of beetles, one for Læsø and one for NE Jutland excluding Læsø, were compiled by a combined effort of several Danish entomologists and the authors of this paper. Three fieldtrips to Læsø were undertaken from 1970 through 1973. This work resulted in a publication on the species of beetles on Læsø (Bangsholt, 1973), which remains the only published checklist of the Coleoptera on Læsø. About 20 years later in 1993–1994 there were three more fieldtrips to the island by Danish coleopterists, including JP. This later collecting effort, Bangsholt (1973), as well as verifying the findings of various coleopterists and information from Danish collections, provided information for a representative list of beetle species on Læsø maintained by JP. Only some of the records on that list have been published (Bangsholt, 1979, 1981, 1983; Hansen et al., 1991, 1994, 1995, 1999; Jørum et al., 2002; Pedersen et al., 2005). The list of rove beetle species on Læsø maintained by JP was here combined with similar information for the rest of Denmark and southern Sweden into a single dataset that includes 1075 species (Tables S1–3).

For each species in this dataset we compiled information on their (1) body length, (2) microhabitat preference, (3) habitat preference and (4) ecological tolerance. For each species all autecological data were gathered from the comprehensive monographs of Freude et al. (1964, 1974), Koch (1989) and especially Assing & Schülke (2012), which take into account bionomic data for the species entire distribution, or at least its Central European part. For as many species as possible we used the newest compilation (Assing & Schülke, 2012) and relied on the older volumes (Freude et al., 1964, 1974; Koch, 1989) mainly when it was the only available source of data, for example for the subfamilies Aleocharinae, Scydmaeninae and Pselaphinae. Microhabitat preference was reduced to the following types: mycetophiles, nidicolis, myrmecophiles, as well as dead wood, vegetation, moss, soil, leaf litter, dung, carrion and compost inhabitants (for definitions of each category see Table S4). For habitat preference, the following categories were used: coastal areas (e.g. beaches), freshwater-edges, heathland, grassland, swamps, rocky terrain, forest, synantropic habitats and arable land (for definitions see Table S4). Every species of rove beetle was assigned to at least one microhabitat and one habitat preference category. Often, species were ascribed to more than one category of microhabitat or habitat preference because most of the species occur in more than one habitat or microhabitat. For each species we also recorded an approximate all averaging ecological tolerance category (gen-

eralist or specialist, for definitions see Table S4). The total body length of a species was noted in mm as an average of its maximum and minimum size given in the species keys of Freude et al. (1964, 1974), and Assing & Schülke (2012).

Data analysis

We compiled a matrix of binary data (presence/absence) for the species occurring in each faunistic region in the study area. To compare the composition of species of rove beetles on Læsø and adjacent mainland sites, we calculated the Sørensen pairwise dissimilarity index (β_{sor}). Because the species richness differed greatly in the different faunistic districts (Table S1), we decomposed the Sørensen dissimilarity index into nestedness-resultant dissimilarity (β_{nes}) and Simpson pairwise dissimilarity (β_{sim}) based on Baselga (2010). Nestedness (β_{nes}) occurs when sites with a low diversity are subsets of sites with high diversity (Wright & Reeves, 1992; Ulrich & Gotelli, 2007), while the Simpson pairwise dissimilarity (β_{sim}) is a measure of turnover or the replacement of species between sites (Qian et al., 2005). The β_{sim} metric is preferable because it is insensitive to differences in species richness among assemblages, thus providing an unbiased estimate of compositional turnover. We used average linkage cluster analysis (UPGMA) to visualize the relationships among faunistic districts. All analyses were carried out in R (R Core Team, 2014) using the functions within the “betapart” package (Baselga & Orme, 2012).

To explore how the species found on Læsø ($n = 328$) differed from those on mainland sites ($n = 1075$) in terms of traits, we compared species assemblages on Læsø and the surrounding mainland for continuous and discrete variables. For continuous (body size) and discrete (ecological tolerance) variables we calculated the mean values of the 328 species recorded on Læsø (obs.) and compared it with the distribution of values obtained by repeatedly sampling 328 species at random from the full dataset 999 times (exp.). Differences between Læsø and mainland assemblages were assessed using standardized effect sizes (SES) $[(\text{mean}(\text{obs.}) - (\text{mean}(\text{exp.}))) / \text{SD}(\text{exp.})]$, where values > 1.96 or < -1.96 are considered significant differences. A similar approach was used for the categorical variables (microhabitat and habitat preference). Here we randomly selected 328 species from the full dataset and calculated the proportion of species contained in each category for 999 iterations. Then, these were compared to the 328 species found on Læsø. In both approaches, the number of faunistic districts where a species occurs was used as weights to maintain the distributional patterns of the species assuming that more common species are better dispersers. SES were used to compare these values and P values were calculated as the fraction of permutation values that were at least as extreme as the observed value.

RESULTS

Relation of Læsø fauna to that on the mainland

The decomposition of the pairwise dissimilarity coefficients revealed that the nestedness component had an overall stronger contribution to the observed dissimilarities between regions ($\text{mean}(\beta_{\text{nes}}) = 0.15$, $\text{mean}(\beta_{\text{sim}}) = 0.09$). This pattern was stronger when Læsø is compared to the other regions ($\text{mean}(\beta_{\text{nes}}) = 0.36$, $\text{mean}(\beta_{\text{sim}}) = 0.08$). The nestedness component shows that Læsø has a high dissimilarity when compared to the rest of the regions. Based on the Simpson pairwise dissimilarity (β_{sim}) and UPGMA clustering, the Swedish and Danish sites can be separated into two distinct clusters. Furthermore, Læsø and NE Jutland

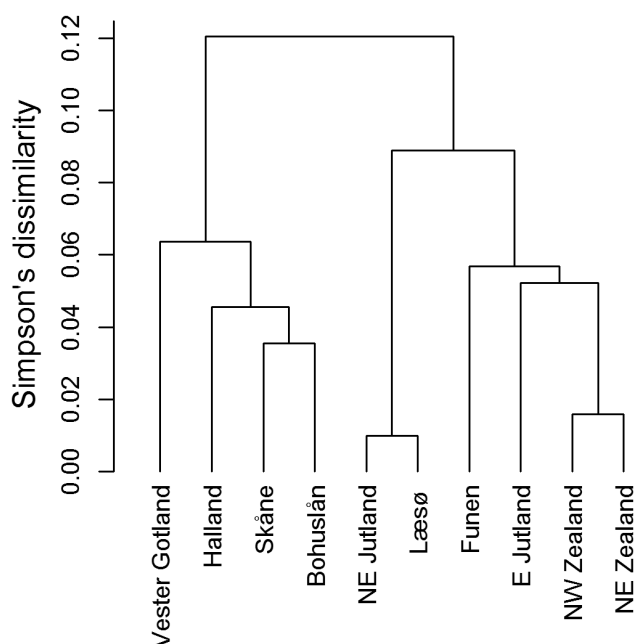


Fig. 3. Differences in rove beetle assemblage between the faunistic regions based on Simpson's pairwise dissimilarity (β_{sim}) and UPGMA clustering.

show almost no dissimilarity due to turnover, indicating that the rove beetle fauna on Læsø is almost completely nested within that of NE Jutland (Fig. 3).

Body size distribution on Læsø compared to that on the mainland

The average body size (measured as full body length) of rove beetles on Læsø ($n = 328$) was 4.56 mm, while the mean average size of 999 samples of 328 randomly selected species of beetles from the whole dataset ($n = 1075$) was 4.37 ± 0.18 mm, which is not significantly different ($SES = 1.05$; $P = 0.14$) (Fig. 4).

Eco-geographic traits of the Læsø fauna compared with those of the mainland fauna

Ecological tolerance of the species assemblage on Læsø was significantly different from those of the random samples of adjacent mainland assemblages for both categories. Ecological generalists were overrepresented on Læsø, while ecological specialists were underrepresented on this island (Fig. 5). The proportion of species on Læsø was significantly different from those on the mainland for all habitat preference categories except swamp associated species (Fig. 6). Species associated with coastal habitats, heathland, grassland, synanthropic habitats and arable land were overrepresented on Læsø compared to mainland areas. On the contrary, species associated with freshwater-edge habitats, rocky habitats and forest were underrepresented on the island. With respect to the proportion of species associated with ant nests, dead wood, moss, vegetation and nidicolous microhabitats there is no statistical difference between Læsø and the mainland (Fig. 7). However, compared with the mainland mean, there was an overrepresentation of Læsø species associated with fungi, dung, carrion and compost piles. On the contrary, species living in leaf

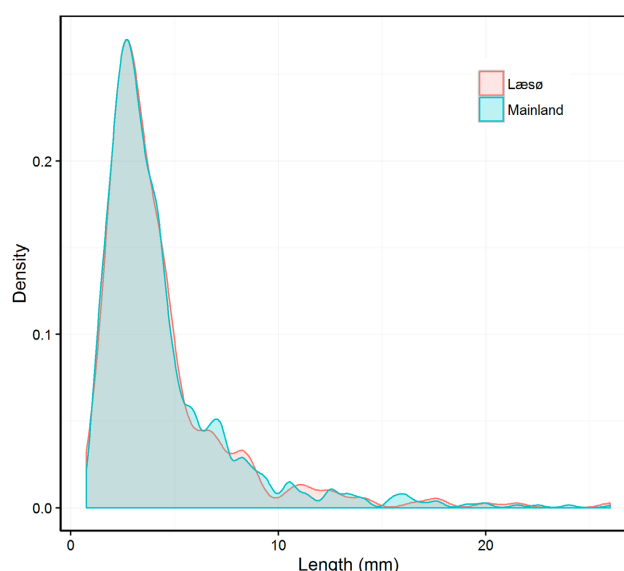


Fig. 4. Body size (length in mm) density plot of rove beetles on Læsø (red) and the mainland (blue).

litter or soil were significantly underrepresented on Læsø, compared to the mainland.

DISCUSSION

The similarity in beetle species composition based on the turnover of species showed that the rove beetle fauna on Læsø is most similar to that in North-Eastern Jutland (Fig. 3) suggesting NE Jutland as the most probable mainland region from which the fauna of Læsø originated. The summer winds in the study area predominantly blow from the west (Cappelen & Jørgensen, 1999) the same direction from which most of the human traffic to the island came, both of which may have facilitated arrivals from this source. Alternatively, if Læsø was populated from elsewhere, or randomly without a predominant source area, its greatest faunistic similarity with NE Jutland may indicate similar environmental conditions that create filters producing similar faunas. Using a phylogenetic framework to determine the dispersal history of populations of each species is the best way to explore this more rigorously. There is such a study for the large flightless ground beetle *Carabus arcensis*, which indicates NE Jutland as a source area for the Læsø populations (Hansen et al., 2018). In any case, the Læsø – NE Jutland cluster in Fig. 3 is in accordance with the proximity of these sites, with their habitat similarity largely determined by their similar sandy and nutrient poor soils. Relevant to the Danish fauna, our results for rove beetles confirms the plausibility of including Læsø within the NE Jutland faunistic district. Our results also indicate that recent sea currents are not acting as a major agent of passive insect dispersal, as they predominantly run from Southeast to Northwest (Turrell, 1992; Paramor et al., 2009) and would in turn promote dispersal from Sweden, which is not supported by this study.

There is no difference in the body size distribution among rove beetles on Læsø and the adjacent mainland (Fig. 4). Presumably the geologically young age of Læsø and its

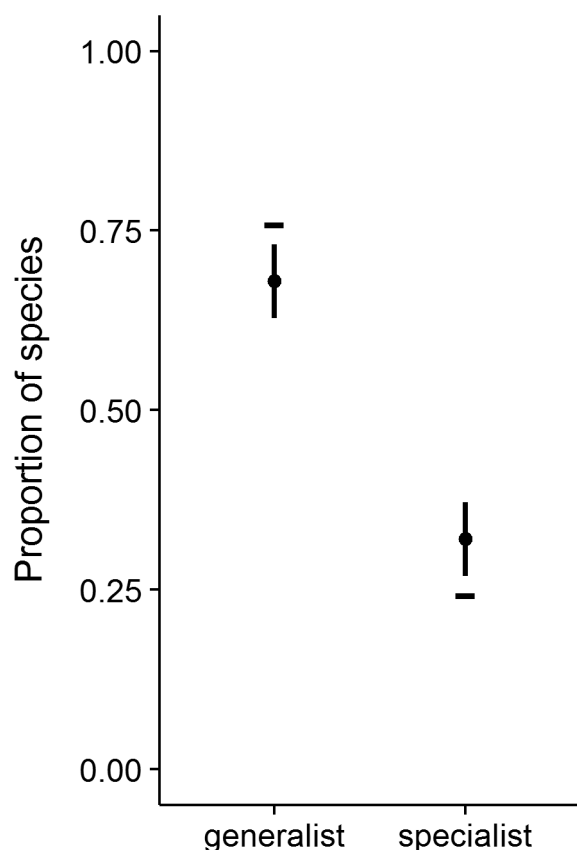


Fig. 5. Proportion of generalist and specialist species on the island of Læsø compared to the null expectation. Null expectation obtained by randomly selecting 328 species from the full dataset (999 iterations) with dots and bars showing the mean and standard deviation, respectively. Black horizontal lines are significantly different from null expectation.

relative proximity to the mainland do not pose an ecological filter for insect body size, something that is reported for significantly older and truly remote oceanic islands (Gillespie et al., 2012). It is presumed that the ecological filtering on this island is for different traits.

Analysis of the ecological traits of rove beetle species present on Læsø and the surrounding mainland shows a statistically significant predominance of ecological generalists over specialists on Læsø (Fig. 5). It remains to be shown that this is because ecological generalists are more prone to disperse, which increases their chances of colonizing other habitats, or if this is due to other factors like the wider ecological niches of generalist species.

There is an ecological filtering at the habitat scale as there is an overrepresentation on Læsø of rove beetle species confined to heathland, grassland and seashores, i.e. habitats that are naturally common on Læsø (Fig. 6) and an underrepresentation of species associated with lake and river banks, or stony areas with rocky outcrops that are rare habitats on Læsø (Fig. 6). In addition, even though a relatively large area of the island is now covered by forest, we found an underrepresentation of forest-associated species on Læsø (Fig. 6). Due to the relatively dry conditions in Læsø forests, mainly represented by coniferous plantations, they may be a much less species-rich habitat for

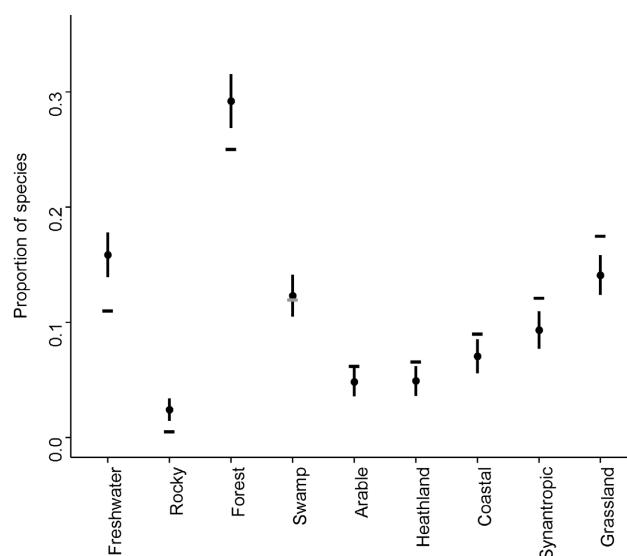


Fig. 6. Habitat preference of rove beetles on the island of Læsø compared to the null expectation. Null expectation obtained by randomly selecting 328 species from the full dataset (999 iterations) with dots and bars showing the mean and standard deviation, respectively. Black horizontal lines are significantly different from null expectation. Grey lines are not significantly different.

rove beetles than their more diverse mainland counterpart with a larger proportion of deciduous trees (Nord-Larsen et al., 2016). It is well-known that the rove beetle fauna of deciduous forests is more rich than in coniferous forests in Europe (Bohac, 1999; Lange et al., 2014). Our findings are also consistent with the hypothesis that recent human induced deforestation of the island during the period of intense salt production (Hansen, 1995) may have eliminated deciduous forest-dependent species, but this needs further study.

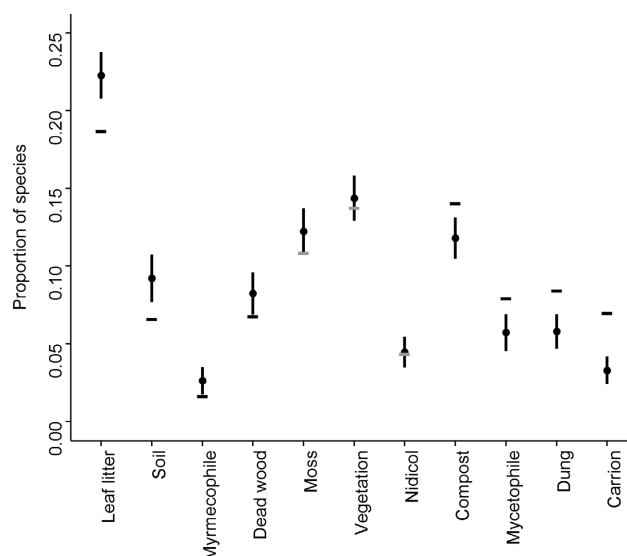


Fig. 7. Microhabitat preference of rove beetles on the island of Læsø compared to the null expectation. Null expectation obtained by randomly selecting 328 species from the full dataset (999 iterations) with dots and bars showing the mean and standard deviation, respectively. Black horizontal lines are significantly different from null expectation. Grey lines are not significantly different.

Overrepresentation of species confined to patchily distributed ephemeral substrate microhabitats such as fungi, dung, carrion or piles of compost indicates that a higher mobility necessary for frequent movements between patches, confers a higher probability of establishment success on Læsø. In turn, such high mobility could have increased the chance of these species reaching the island as opposed to less mobile species. This agrees with studies showing that life history traits, such as development of functional wings and evolution of efficient flight promote efficient dispersal (Roff, 1990; Bonte et al., 2012).

It is yet to be tested whether the underrepresentation of ecological specialists and proportional overrepresentation of ecological generalists on Læsø corresponds to a relatively early stage of colonization of a newly formed oceanic island or whether the small size of the island limits the establishment of specialists. A possible way of testing this hypothesis would be to examine whether on islands of different ages there is a change from predominantly generalist to specialists species with increasing age (Wilson, 1961). The Baltics offer the possibility of conducting such a study, as there are many islands of different ages, sizes, and natural history, and their faunas are relatively well-known.

In conclusion we found a significant microhabitat-based filtering of the fauna established on the island studied, which may indicate that life histories of some species make them more or less prone to disperse and colonize islands. The effect of the anthropogenic deforestation of Læsø in connection with the salt production is still unknown, but seems, based on our results, that the fauna has not yet fully recovered. Similarly, the processes leading to the overrepresentation of ecological generalist on the island, needs further study. We should stress that this is the first attempt to evaluate the family Staphylinidae in an eco-faunistic study in a mainland-island system in Northern Europe. It clearly and quantitatively shows patterns that are reported or discussed for other groups of organisms, but not necessarily based on the same amount of data or precision. The set of data collected, patterns, hypotheses and rove beetles as a model group, hopefully can help in the design of future studies.

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Supplementary files:

Table S1 (<http://www.eje.cz/2018/025/S01.pdf>). Distributions and tolerances.

Table S2 (<http://www.eje.cz/2018/025/S02.pdf>). Habitat preferences.

Table S3 (<http://www.eje.cz/2018/025/S03.pdf>). Microhabitat preferences.

Table S4 (<http://www.eje.cz/2018/025/S04.pdf>). Descriptions of categories.